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Natural Selection: How Selection on Behavior Interacts with Selection on Morphology

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Can behavior accelerate or buffer morphological evolution? A recent experiment in a natural setting shows that selection acts on behavior and morphology, but acts on each trait independently of the other.

Behavior, like morphology, can vary among individuals, be heritable, contribute to fitness, and hence be subject to evolution by natural selection. For a long time, however, behavior has occupied a special place in the minds of evolutionary biologists, who have debated whether the evolution of behavior accelerates or inhibits the evolution of non-behavioral traits [1,2]. Much of this attention has focused on behavior and morphology: do these features represent different facets of the phenotype that evolve together or does the evolution of one of these types of traits create the context for the subsequent evolution of the other? Lapiedra *et al.* [3] have shed light on these questions with a beautifully designed and executed experimental study of selection in the lizard *Anolis sagrei* (Figure 1).

Any investigation of these questions must overcome some considerable challenges. The critical ingredients necessary for quantifying how behavior and morphology jointly affect fitness include identifying behaviors that potentially have a strong impact on fitness, assaying and establishing that there are repeatable differences among individuals in how these behaviors are manifested, quantifying features of morphology that also affect fitness, and analyzing the joint contribution of morphology and behavior to fitness. Quantifying behavior poses its own challenges. Behavior is phenotypically plastic [4], often influenced by the prior experience of individuals [5], and often sensitive to the context in which it is measured [6].

Given these challenges, it is no surprise that questions about the joint evolution of behavior and morphology have been answered differently in different studies. Brodie's [7] study of garter snakes (*Thamnophis ordinoides*) pointed to the integrated evolution of morphology (color pattern) and escape behavior. He found that some combinations of behavior and color pattern had higher probabilities of survival than others. The fitness consequences of a given color pattern (behavior) depended upon the type of behavior (color pattern). On the other hand, studies of behavioral thermoregulation and habitat use in lizards pointed to how behavior acted as a buffer of selection on other traits.

Huey *et al.* [8] showed that individuals from high-elevation populations of the lizard *Anolis cristatellus* in Puerto Rico were able to reduce the effects of the cooler environment and sustain performance by spending more time in the sun. Behavior thus reduced the necessity for the evolution of metabolism. Munoz and Losos [9] extended this approach by studying habitat use and morphology in populations of *Anolis* lizards from low and high elevations on Hispaniola. High elevation lizards increased their exposure to sun by shifting from perching in trees to perching in boulders. This change in habitat in turn selected for the evolution of head shape and limb dimensions. Behavior thus buffered metabolic evolution while at the same time facilitating morphological evolution.

These and other studies have made compelling cases for adaptive evolution of behavior and morphology. They are limited, however, in their ability to test fully whether the evolution of behavior catalyses or retards the evolution of morphology. This is because they are retrospective in nature, which limits the ability to infer the actual cause and effect

Figure 1. *Anolis sagrei*, the subjects of this experiment.
This photo illustrates the marked morphological differences between the male (above) and female (below). Differences in morphology are matched by differences in behavior. This research revealed that the near-term selection associated with the presence or absence of the predator was much stronger on females than males but at present we do not know why. (Photo credit: Manuel Leal.)

relationships between each type of trait. To do so, we need carefully controlled experiments in nature that enable us to watch the process as it unfolds. Lapiedra *et al.* [3] offer us precisely such an experiment with their study of the brown anole, *Anolis sagrei*.

These small lizards forage for food on the ground and on lower branches of shrubs. *Leiocephalus carinatus* is a larger lizard species that preys on *A. sagrei* that it finds on the ground; *A. sagrei* can escape them by ascending trees and shrubs. Exploratory behavior and a tendency to spend time on the ground are two behaviors that ought to affect fitness in the presence or absence of predators. Initiating exploration and spending more time on the ground, as opposed to hiding or ascending a shrub, will enable individuals to acquire more food, but also increase their exposure to predators. Body size and relative limb length also affect how well they perform in different habitats. Being longer limbed and larger enables *Anolis* lizards to move more rapidly on the ground, but shorter limbs and smaller body sizes are better suited for spending time in shrubs.

Lapiedra *et al.* [3] captured 273 *A. sagrei* on larger islands and scored each of them for two behaviors. To do so, they first gave them visual contact with a predator and then placed them in an opaque box in an outdoor arena. After a three-minute habituation period, they lifted the box and measured the time until the lizard emerged from under the box to explore its surroundings. They also measured how long each lizard remained on the ground before either hiding or ascending a perch. The authors measured these behaviors twice on a subset of lizards ($n = 80$) to verify that the variation among individuals was repeatable. They x-rayed each lizard for morphological measurements, marked them for individual recognition, then released them on eight small, lizard free cays (Figure 2). After a week, they released *L. carinatus*, the predator, on four of the eight cays. After four months they collected all surviving *A. sagrei*, identified them, and analyzed whether their behavior and/or morphology influenced their survival. While this study focused on an episode of selection, not evolution, past experiments have shown the direction of selection on *A. sagrei* is a good predictor of the direction of its evolution [10].

Male *A. sagrei* lizards are larger than females (Figure 1) and have different patterns of habitat use, so Lapiedra *et al.* [3] predicted that the sexes might differ in how they responded to life with and without predators. When predators were present, both sexes suffered higher mortality rates and spent less time on the ground and more in the shrubs. Males were less affected by predators and their responses fell short of statistical significance when compared to the responses on predator-free islands.

The story was very different for females. When predators were absent, selection significantly favored individuals that had initiated exploratory behavior more quickly in the behavioral trials and those who had relatively longer legs. In contrast, when predators were present, selection favored individuals that spent less time in the open in the behavioral

Figure 2. Example of a small cay that represents the 'experimental unit'.
This experiment was performed on eight such cays (sandy islands). They are large enough to sustain a population of *Anolis sagrei*, but small enough to make it practical to fully census them and follow the fate of every individual in the population.

trials and those who were smaller in body size. There was a clear cost to moving up into the shrubs to avoid predators: females from islands with predators were in poorer condition (weighed less relative to their length) than females from islands without predators.

How did selection act on morphology and behavior? First, while each aspect of behavior and morphology was under selection, selection acted independently on them. There was no indication that the value of an individual's behavior depended upon its morphology or vice-versa. Second, the strength of selection on behavior and morphology depended heavily on context. On islands without predators, 13.9% of the variation in survival was attributable to behavior (shorter lag before exploration) and 19.1% to morphology (longer legs). On islands with predators, 22.5 % of the variation is attributable to behavior (avoidance of the ground) but only 9.8% was attributable to morphology (smaller body size).

Why is the work of Lapiedra *et al.* [3] important? For one reason, the work described here was a well-controlled experiment in nature with statistical controls for what the authors could not equalize. For example, some of the *A. sagrei* used in the experiment came from islands with *Leiocephalus* and others did not. The authors were able to show that the island of origin had no effect on the results. For another, the authors' show that the effects of behavior on survival were a function of individual differences, not momentary behavioral decisions. They did so because they performed their assay of behavior before the experiment was initiated and showed that the behavioral differences among individuals were repeatable.

Taken together, these virtues reveal the importance of looking at the dynamics of selection, rather than just the end product. The dynamics revealed that selection on behavior and morphology were statistically independent of one another. The end product, which is what prior studies have examined, would have shown that behavior and morphology evolved together, which would have led naturally to the conclusion that the evolution of behavior either buffered (in the presence of predators) or accelerated (in the absence of predators) morphological evolution. This new study reveals instead that behavior and morphology are different features of the phenotype that can be selected independently of one another.

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Development: Cell Polarity Is Coordinated over an Entire Plant Leaf

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Models of leaf development have long predicted the existence of an organ-wide polarity field. Now, a robust analysis in a developing *Arabidopsis* leaf reveals the presence of a general and persistent cell polarity coordinated over the entire leaf.

In the spring, leaves burst forth with diverse shapes and sizes. These leaves can be compound with many leaflets, like those of a tomato, or simple and smooth, like those of a lilac. These diverse plant forms are thought to be made by tuning or variably applying developmental mechanisms that are common across plants [1–4]. Studying how these mechanisms can be tweaked to generate diverse leaf forms raises an even greater question: how does any organ reliably